

**HOST PLANT PREFERENCES OF  
*ACANTHOSCELIDES AUREOLUS* (HORN)  
(COLEOPTERA: BRUCHIDAE)**

WAYNE R. OWEN

Graduate Group in Ecology, University of California  
Davis, California 95616<sup>1</sup>

*Abstract.* — The discrimination of *Acanthoscelides aureolus* Horn (Coleoptera: Bruchidae) among individuals of its host plants, *Astragalus kentrophyta* var. *implexus* (Fabaceae), was investigated using a path analytical model that included seven demographic variables. Seed number proved to be the plant trait that contributed most to the rate bruchid use among host individuals. Seed number also exerted an important indirect effect on the correlations between the rate of bruchid use and the other variables in this analysis.

*Key Words.* — Insecta, Bruchidae, *Acanthoscelides aureolus*, *Astragalus kentrophyta* var. *implexus*, path analysis, oviposition preference

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*Acanthoscelides aureolus* Horn (Coleoptera: Bruchidae) is a generalist seed-eating bruchid that uses the seeds of host plants across a broad range of taxonomic affinities (Johnson 1970). At high elevations in the White Mountains of Inyo and Mono Counties in eastern California, *A. aureolus* uses the seeds of an alpine cushion plant, *Astragalus kentrophyta* var. *implexus* (Fabaceae) (hereafter referred to as Aki), to the exclusion of all other hosts (Owen 1991a). *A. aureolus* is the only predispersal consumer of Aki seeds at alpine elevations in the White Mountains (Owen 1991b). The size of the study population of *A. aureolus* varies greatly from year to year (Owen 1991b); a commonplace feature among species of seed eating insects with narrowly defined diets (Janzen 1970, Huffaker et al. 1984).

Patterns of predispersal seed predation have important demographic consequences for populations of flowering plants. By reducing the number of seeds released to the environment, seed-eating insects affect the density of propagules in the dispersal range of each parent plant. In turn, the recruitment of adults into the host population may be adversely affected by either a reduction in the absolute number of seeds in the soil or by decreasing the likelihood of propagules reaching safe sites (Harper 1977).

Because seed predators can have a profound impact on their host species (Janzen 1971, 1981; Louda 1982; Fenner 1985), knowledge of the criteria by which female insects discriminate among potential hosts would be especially useful in the management of rare plant species. Because several species of *Astragalus* in North America experience significant fecundity losses due to seed predation (e.g., Alverson 1985, Smithman 1988, Wright 1988, Lesica & Elliott 1989, Rittenhouse 1990), an analysis of the *A. aureolus*/Aki system could potentially serve as a robust model for the analysis of other bruchid/legume systems.

Seed predation patterns may be the result of the dispersal pattern of the insect or may be due to choices made by ovipositing females. Discrimination among

<sup>1</sup> Mailing address: Boise National Forest, 1750 Front Street, Boise, Idaho 83702.

potential oviposition sites may be influenced by a variety of host plant attributes including fruit color (Riedl & Hislop 1985, Owens & Prokopy 1986), fruit size (Messina 1990), leaf size (Whitham 1978, 1980), plant or shoot size (Everly 1959, Rausher 1983, Fritz & Nobel 1989, Cipollini & Stiles 1991), and flowering phenology (Feeny 1976, Pettersson 1991).

I investigated the rates of seed predation by *A. aureolus* on a group of Aki plants in the White Mountains. Seed predation at this site varies significantly and non-randomly among individuals (0–100%, Owen 1991b) suggesting that females are discriminating among hosts (Rausher 1983). This discrimination is probably not due to differences in phenology among host individuals because Aki flowers and fruits continuously throughout the short growing season in the White Mountains (Owen 1991b). Furthermore, because the chemical constitution of a species' seeds tends to be very uniform within populations (Janzen 1978), it is unlikely that bruchids would discriminate among host plants on the basis of seed quality. Here, I test the importance of physical/reproductive characteristics among Aki individuals to the discrimination by ovipositing *A. aureolus* females. This particular bruchid/*Astragalus* interaction is interesting because of the unusual and severe nature of the environment that these species share. This paper presents an analysis of the relationship between the level of bruchid infestation and physical/reproductive attributes of Aki over a two year period.

#### MATERIALS AND METHODS

I randomly selected a group of 80 Aki plants on the alpine dolomite barrens of Sheep Mountain in the White Mountains, Mono County, California (elevation 3620 m) for study. Little is known about the ways in which species of *Acanthoscelides* select oviposition sites. Cipollini & Stiles (1991) report that *A. obtectus* females select among *Phaseolus* flowers on the basis of their not having been previously visited by an ovipositing female, and that they do not discriminate among oviposition sites on the basis of expected seed size. Green & Palmbald (1975) report that *Acanthoscelides fraterculus* selects among potential *Astragalus* species for oviposition on the basis of their flowering phenology, and physical and chemical differences between the fruits of potential host species. In light of a general lack of a priori expectations as to which host plant traits might be most important to a female bruchid in her search for oviposition sites, I monitored seven demographic characteristics (Table 1) that could reasonably be assumed to be the basis of discrimination among host plants by ovipositing female *A. aureolus* throughout the 1989 and 1990 growing seasons. Plant size was measured as the area (mm<sup>2</sup>) covered by individual cushions at the beginning of each growing season. At the end of each growing season all fruits and seeds produced on each plant were collected and individually weighed. Seed dispersal occurs very late in the growing season, is passive and very limited in distance (Owen 1991b), so I am confident that I was able to harvest every seed produced by every plant. The vigor of each plant was estimated as its relative annual growth (i.e., the total growth in area during a season divided by the initial plant size). Each seed produced by the 80 Aki plants was individually inspected for the evidence of predation. Because *A. aureolus* larvae leave a characteristic scar on seeds, their presence or absence can be unequivocally determined by visual inspection. Furthermore, microscopic inspection of several hundred Aki flowers showed that *A. aureolus* eggs and larvae



Table 1. Comparison of mean trait values across in the two years of the experiment.

	1989		1990		<i>t</i> <sup>b</sup>	<i>P</i>
	Mean	CV <sup>a</sup>	Mean	CV		
Plant size (mm square)	6580.04	57.28	7460.22	54.71	-4.94	0.01
Fruit number	24.53	118.50	29.27	110.45	-0.98	ns
Seed number	28.60	117.40	33.06	109.82	-0.91	ns
Fruit weight (milligrams)	1.54	23.50	1.46	24.40	2.03	0.05
Seed weight (milligrams)	1.78	17.99	1.68	23.63	2.26	0.05
Seed/fruit	0.98	57.00	1.04	40.95	-0.29	ns
Vigor (growth/size)	0.23	146.07	0.19	179.13	1.18	ns

<sup>a</sup> The coefficients of variation (CV) are given to indicate the relative variability of each character.

<sup>b</sup> Differences in the means tested with two-tailed paired Student's *t*.

are not present in abortive flowers (Owen 1991b). I am, therefore, confident that I have accounted for all oviposition events made by *A. aureolus* on the 80 Aki plants.

The effect of each plant trait on the level of seed predation was investigated with a path analytical model (Dewey & Lu 1959, Sokal & Rohlf 1981). A path analysis allows the simultaneous consideration of several intercorrelated variables in a linear regression frame work. In the path analysis, a cause and effect relationship between the predictor variables (the seven demographic characteristics presented in Table 1) and the criterion variable (rate of bruchid attack) is assumed. The standard partial correlation coefficients from the multiple linear regression are presented as path coefficients, and as such represent the direct influence of those variables on the criterion variable. All unknown (residual) factors are combined into a coefficient of nondetermination (*U*), which reflects the fraction of the model variance unaccounted for by the predictors. Because the path analysis requires data to conform to the distributional assumptions of linear regressions, the appropriate transformations have been made to improve the normality of some variables. Separate paths are constructed for the 1989 and 1990 data.

The rate at which *A. aureolus* uses *Astragalus* seeds is expressed as the ranked percentage (Conover & Iman 1981) of seeds per plant used by *A. aureolus*. Ranked rates of seed use best serve the objective of the model in that ovipositing females may not always choose the "best" host plant but must rank the quality of and choose among the host plants that they encounter (Rausher 1983).

Because many of the predictor variables are intercorrelated (Table 2), each may exert a telling influence on the correlation between other predictors and the criterion variable. The potential indirect effects of variables can be investigated by using the normal equations originally used to determine the path coefficients. For example, for the first variable in this analysis,

$$r_{1Y} = P_{1Y} + r_{12}P_{2Y} + r_{13}P_{3Y} + r_{14}P_{4Y} + r_{15}P_{5Y} + r_{16}P_{6Y} + r_{17}P_{7Y}.$$

In this expression, *r* is the coefficient of correlation between variables *i* and *j*, *Y* is the criterion variable, and *P* represents standard regression coefficients. There-

Table 2. Correlations among plant traits used in the path analysis. Values above the diagonal are based on 1989 data, those below the diagonal are for 1990 data.

	Plant size	Fruit number	Seed number	Fruit weight	Seed weight	Seeds/fruit	Vigor
Plant size	—	0.403** <sup>a</sup>	0.532**	0.015	0.025	-0.006	-0.255*
Fruit number	0.621**	—	0.509**	0.071	0.201	-0.341**	0.117
Seed number	0.585**	0.966**	—	0.035	0.177	0.253*	-0.017
Fruit weight	-0.053	0.054	0.086	—	0.368**	-0.010	0.155
Seed weight	0.035	0.102	0.076	0.284*	—	-0.070	0.255*
Seeds/fruit	-0.036	0.007	0.209	0.260*	0.100	—	0.230*
Vigor	-0.130	-0.069	-0.039	0.043	0.052	0.137	—

<sup>a</sup> Significance levels: \* =  $P < 0.05$ ; \*\* =  $P < 0.01$ .

fore,  $r_{1Y}$  is the correlation between predictor variable 1 and the criterion variable and  $P_{1Y}$  represents the direct effect (path coefficient) of predictor variable 1 on the criterion variable  $Y$ . The indirect effects are represented by the products  $r_{ij}P_{jY}$ . In the example above, a small correlation between predictor variables 1 and  $j$  will exert a minimal influence on the overall correlation between predictor 1 and the criterion variable by decreasing the contribution of  $r_{ij}P_{jY}$  to  $r_{1Y}$ . Conversely, when  $r_{1j}$  is large,  $r_{ij}P_{jY}$  exerts a nontrivial effect on  $r_{1Y}$ . An analysis of the indirect effects is crucial to gaining a complete understanding of the relationship between the predictor variables and the criterion variable.

## RESULTS AND DISCUSSION

Mean values and coefficients of variations for the seven plant traits used in this analysis are presented in Table 1. Paired Student's  $t$ -tests were used to discern whether trait values differed significantly between 1989 and 1990. Not surprisingly, plant size was significantly greater in 1990 than in 1989 (a reflection of annual growth). There were significant differences in the mean (within individual) weight of fruits and seeds between years (Table 1). Although 1989 reproductive products were heavier, the difference between years is no more than 0.1 mg (6% change). Although the coefficients of variation for mean seed size are small (Table 1), within-individual seed weights vary by as much as a factor of eight (Owen 1991b). This pattern of greater variation within, rather than among, individuals for seed size variation would make discrimination very difficult among host plants by the female bruchid on the basis of seed size. The number of fruits and seeds produced by individuals did not differ significantly between years (Table 1). In contrast, the number of fruits and seeds produced varied widely among test individuals. Individual plants produced 0–165 and 0–187 fruits, and 0–179 and 0–150 seeds in 1989 and 1990, respectively. Vigor, the relative growth rate of individuals, did not differ significantly between years, but varied widely among individuals. In both years, some individuals decreased in size by just over 50%, but others increased by approximately 70%. Finally, the number of seeds per fruit was consistent between years and among individuals.

The correlations among the demographic variables used in the path analysis are presented in Table 2. There are several significant correlations, most notable are the associations between fruit and seed number and plant size. The correlation between fruit and seed weight is likewise consistent across years. Other correlations

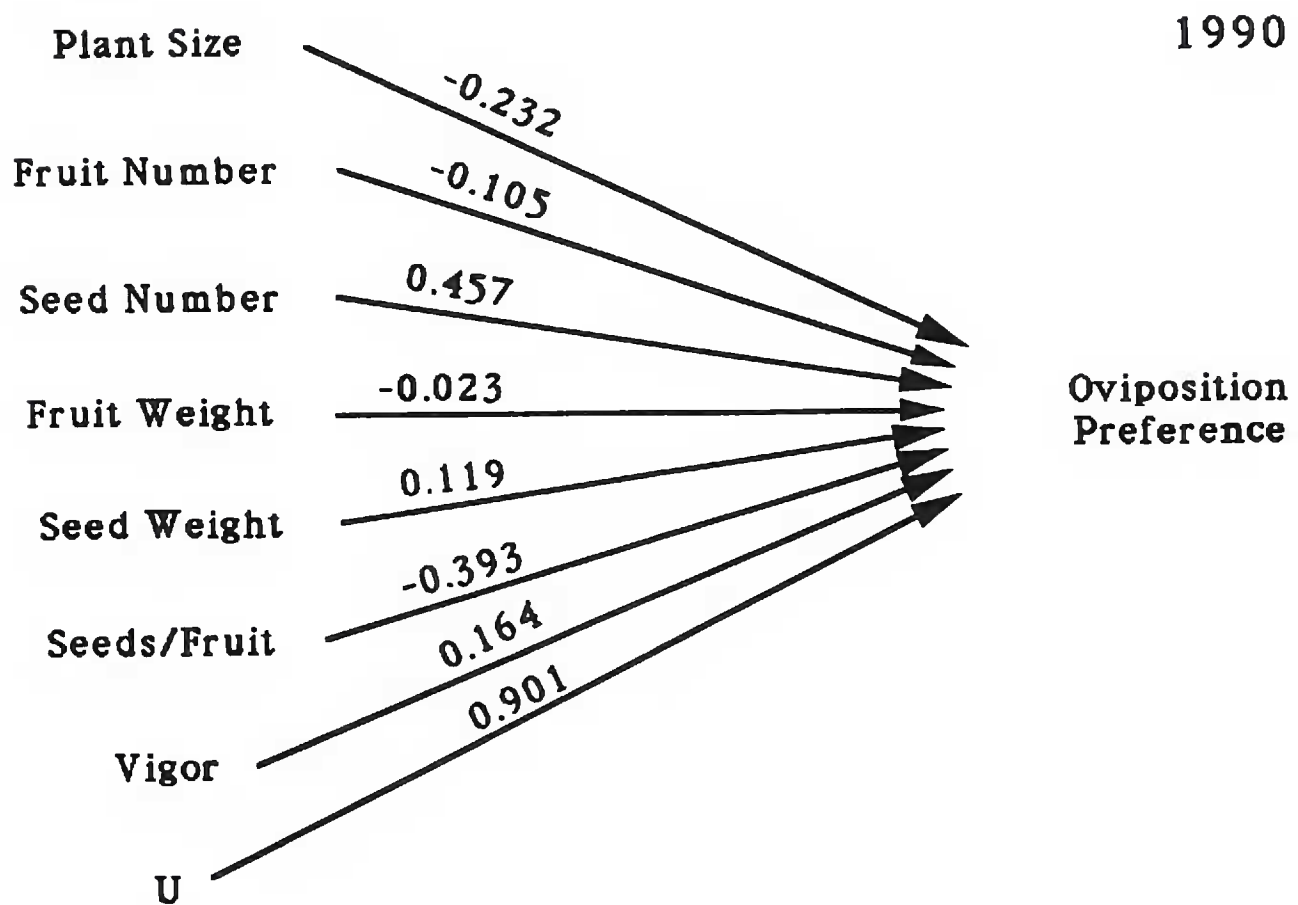
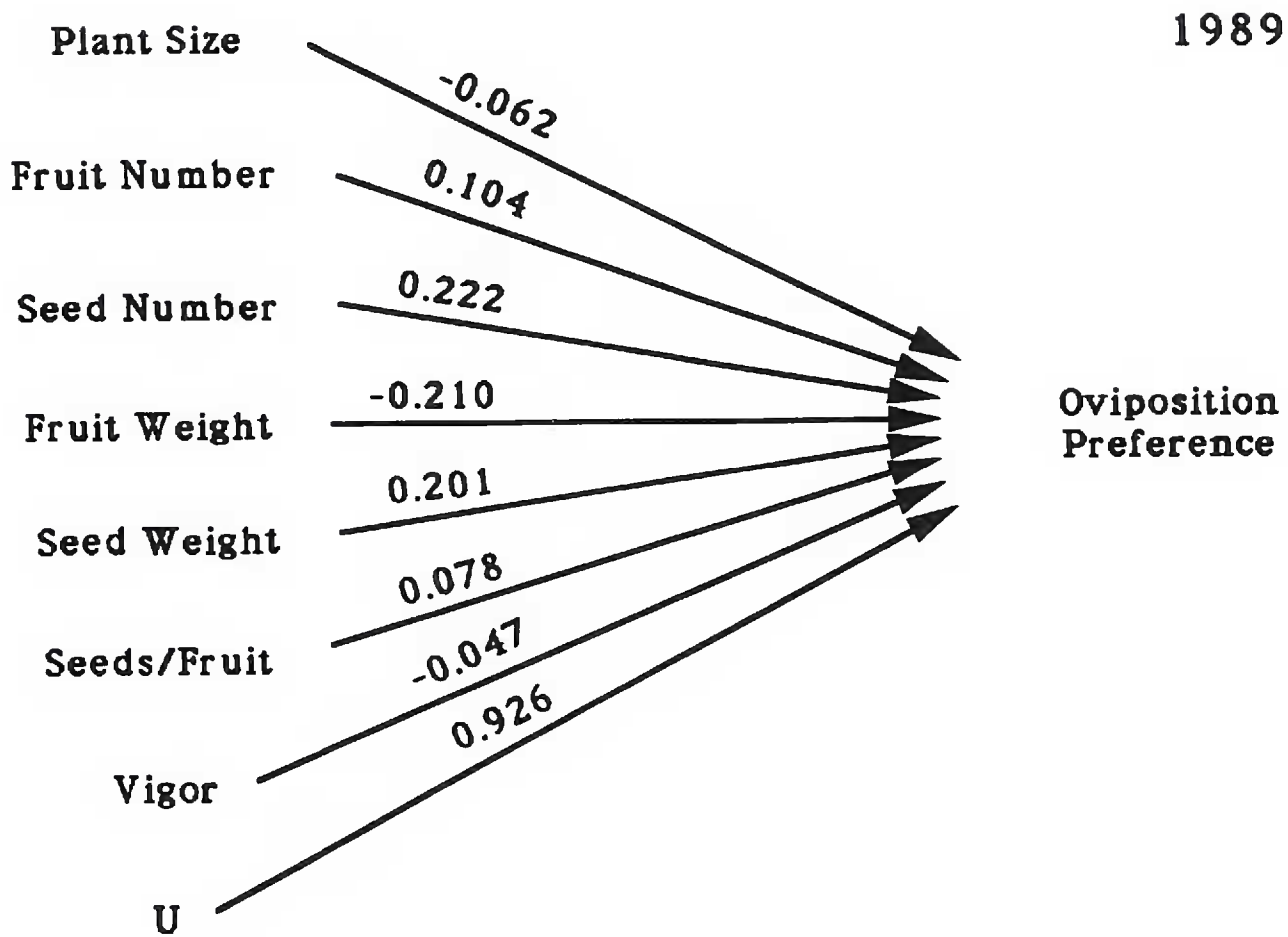


Figure 1. Path coefficients (direct effects) for predictor variables on the ranked percentage of seeds consumed by bruchid larvae in 1989 and 1990. Cross correlations among predictor variables are presented in Table 2. *U* represents the coefficient of nondetermination, a residual factor for the path model.



occur only in either 1989 or 1990. Such transient correlations are difficult to interpret alone and may, in fact, be spurious.

The results of the path analyses for 1989 and 1990 are presented in Fig. 1. Because there is no way of establishing statistical significance for path coefficients (but see Mitchell 1991), their value must be judged in accordance with their individual magnitudes. The large residual factors ( $U$ ) indicates that most of the variation in bruchid infestation rate among plants was not accounted for by the path analysis. Although the paths for seed number consistently have the greatest coefficients, there are some potentially important inconsistencies in the results for the other predictor variables. The importance of fruit weight changes by an order of magnitude between years. Fruit weight becomes less important to the model in 1990, when fruit weight is significantly less compared to 1989. This correlation might be due to heavier fruits, with thicker walls, being more difficult to oviposit in than are lighter fruits with correspondingly thinner walls. The direct effect of fruit number, seeds per fruit, and vigor changes sign between years, indicating that they are poor predictors of host quality. The advantage of monitoring bruchid selection of host plants for more than one year is evidenced in the path coefficient for seeds per fruit (Fig. 1). In 1989 that direct effect was trivial (0.078), but in 1990 it was second in magnitude only to seed number ( $-0.393$ ). Seed weight was consistently important in host plant selection in both years. Plant size, although consistently negatively associated with host plant preference, varied greatly in magnitude between years.

The effects of the predictor variables, through their influence on one another, are presented in Table 3. In Table 3, the correlation coefficients between individual predictors and bruchid infestation rates ( $r_{iY}$ ) are presented as the sums of the path coefficients ( $P_{iY}$ ) and the indirect effects ( $r_{ij}P_{jY}$ ). These decompositions show that most variables contribute very little to the correlations between predictors and criterion variables and consequentially do not substantially affect individual correlations among predictors and bruchid use ( $r_{iY}$ ). In contrast, the indirect effect of seed number ( $r_{i3}P_{3Y}$ ) consistently exerts an important influence on the relationship between predictors and the ranked rate of *A. aureolus* infestation.

The combined results of the path analysis and the decomposition of the normal equations strongly supports seed number as the most important trait of Aki to *A. aureolus* females when making oviposition choices. However, at the time of oviposition the size of seed crop of each plant is ambiguous; this suggests that either the bruchids are cueing on some plant attribute, which is correlated with seed production, that is not considered in this analysis, or that they are somehow using the history of seed production for a given plant as an indicator of its future productivity. Table 4 provides the results of simple linear regressions for the values of each predictor variable in 1990 on the 1989 trait values. Plant size is the trait that is most consistent across years ( $r^2 = 0.877$ ). However, the density of seeds produced by individual plants (seeds produced/plant size) is inconsistent across years ( $t = 0.463$ ,  $P = 0.645$ ), indicating that plant size is a poor predictor of seed production. Seed number is the next most consistent plant characteristic in Aki ( $r^2 = 0.407$ ). Additionally, seed production by Aki is exceptionally stable in the face of environmental fluctuations. In an experiment using 189 Aki plants, no changes in fecundity were detected in response to supplemental watering, herbivore abatement, fertilization, or the removal of competitors (Owen 1991b).

Table 3. Indirect effects on the correlation between individual predictor variables and bruchid infestation rate.

Category/effect	Variable	Value	
		1989	1990
Plant Size vs. Bruchid Infest. Rate		0.112	-0.032
Direct effect	$P_{1Y}$	-0.062	-0.232
Indirect effect of fruit number	$r_{12}P_{2Y}$	0.042	-0.065
Indirect effect of seed number	$r_{13}P_{3Y}$	0.118	0.267
Indirect effect of fruit weight	$r_{14}P_{4Y}$	-0.003	0.001
Indirect effect of seed weight	$r_{15}P_{5Y}$	0.005	0.004
Indirect effect of seeds/fruit	$r_{16}P_{6Y}$	-0.001	0.014
Indirect effect of vigor	$r_{17}P_{7Y}$	0.012	-0.021
Seed Number vs. Bruchid Infest. Rate		0.291	0.139
Direct effect	$P_{3Y}$	0.222	0.457
Indirect effect of plant size	$r_{31}P_{1Y}$	-0.033	-0.136
Indirect effect of fruit number	$r_{32}P_{2Y}$	0.053	-0.101
Indirect effect of fruit weight	$r_{34}P_{4Y}$	-0.007	0.002
Indirect effect of seed weight	$r_{35}P_{5Y}$	0.036	0.009
Indirect effect of seeds/fruit	$r_{36}P_{6Y}$	0.020	-0.082
Indirect effect of vigor	$r_{37}P_{7Y}$	0.001	-0.006
Seed Weight vs. Bruchid Infest. Rate		0.165	0.097
Direct effect	$P_{5Y}$	0.201	0.119
Indirect effect of plant size	$r_{51}P_{1Y}$	-0.002	-0.008
Indirect effect of fruit number	$r_{52}P_{2Y}$	0.021	-0.011
Indirect effect of seed number	$r_{53}P_{3Y}$	0.039	0.035
Indirect effect of fruit weight	$r_{54}P_{4Y}$	-0.077	-0.007
Indirect effect of seeds/fruit	$r_{56}P_{6Y}$	-0.006	-0.040
Indirect effect of vigor	$r_{57}P_{7Y}$	-0.012	0.009
Vigor vs. Bruchid Infest. Rate		0.014	0.135
Direct effect	$P_{7Y}$	-0.047	0.164
Indirect effect of plant size	$r_{71}P_{1Y}$	0.016	0.030
Indirect effect of fruit number	$r_{72}P_{2Y}$	0.012	0.007
Indirect effect of seed number	$r_{73}P_{3Y}$	-0.004	-0.018
Indirect effect of fruit weight	$r_{74}P_{5Y}$	-0.033	-0.001
Indirect effect of seed weight	$r_{75}P_{5Y}$	0.051	0.006
Indirect effect of vigor	$r_{76}P_{6Y}$	0.018	-0.054
Fruit Number vs. Bruchid Infest. Rate		0.186	0.190
Direct effect	$P_{2Y}$	0.104	-0.105
Indirect effect of plant size	$r_{21}P_{1Y}$	-0.025	-0.144
Indirect effect of seed number	$r_{23}P_{3Y}$	0.113	0.442
Indirect effect of fruit weight	$r_{24}P_{4Y}$	-0.015	0.001
Indirect effect of seed weight	$r_{25}P_{5Y}$	0.041	0.012
Indirect effect of seeds/fruit	$r_{26}P_{6Y}$	-0.027	-0.003
Indirect effect of vigor	$r_{27}P_{7Y}$	-0.006	-0.011
Fruit Weight vs. Bruchid Infest. Rate		-0.130	-0.039
Direct effect	$P_{4Y}$	-0.210	-0.233
Indirect effect of plant size	$r_{41}P_{1Y}$	-0.001	0.012
Indirect effect of fruit number	$r_{42}P_{2Y}$	-0.007	-0.006
Indirect effect of seed number	$r_{43}P_{3Y}$	0.008	0.039
Indirect effect of seed weight	$r_{45}P_{5Y}$	0.074	0.034
Indirect effect of seeds/fruit	$r_{46}P_{6Y}$	-0.001	-0.102
Indirect effect of vigor	$r_{47}P_{7Y}$	-0.007	0.007
Seeds/Fruit vs. Bruchid Infest. Rate		0.076	-0.262
Direct effect	$P_{6Y}$	0.078	-0.393
Indirect effect of plant size	$r_{61}P_{1Y}$	<0.001	0.008

Table 3. Continued.

Category/effect	Variable	Value	
		1989	1990
Indirect effect of fruit number	$r_{62}P_{2Y}$	-0.036	-0.001
Indirect effect of seed number	$r_{63}P_{3Y}$	0.056	0.096
Indirect effect of fruit weight	$r_{64}P_{4Y}$	0.002	-0.006
Indirect effect of seed weight	$r_{65}P_{5Y}$	-0.014	0.012
Indirect effect of vigor	$r_{67}P_{7Y}$	-0.011	0.022

Fruit and seed weight are likewise consistent among Aki individuals across years (Table 4), although there are significant between-year differences in population wide mean values of these traits (Table 1). Further complicating the reliability of fruit and seed weight as indicators of host quality are the generally small correlations between these traits and seed number (Tables 2 and 4). Finally, although the path coefficients for fruit and seed weight are the same magnitude as the path for seed number in 1989 (Fig. 1), their relative importance declines dramatically in 1990 suggesting instability in those traits that would not favor their use as a guide to host plant quality.

It is not surprising that *A. aureolus* would discriminate among potential hosts based on consistently high rates of fecundity. There should, however, be a cost incurred by Aki individuals in being consistently selected as an oviposition site for *A. aureolus*. I suggest that plants that are subject to chronic seed predation could reduce predation levels by increasing their interannual variance in seed production. This is commonly accomplished by the occasional production of large numbers of offspring, and producing very few offspring in intervening years (i.e., masting, see Janzen 1969). Although common among tree species, masting does not occur among herbaceous perennials in general (Fenner 1985), or in Aki specifically (Owen 1991b). The consequence of consistent seed production is chronic and, in some cases, heavy reductions in fecundity. For Aki, regressions of the number of seeds that escape predation on the total number produced in both 1989 and 1990 have slopes significantly less than, but very near, unity (Table 5). Consequently, greater seed production does not lead to proportionally greater survivorship among the annual progeny cohort of each plant. This pattern may be

Table 4. Results of simple linear regression analyses comparing predictor trait values between 1989 and 1990.

Predictor	F	P	r <sup>2</sup>
Plant size <sup>a</sup>	550.05	0.0001	0.877
Fruit number	9.10	0.0035	0.107
Seed number	51.55	0.0001	0.407
Fruit weight	36.36	0.0001	0.339
Seed weight	22.26	0.0001	0.247
Seed/fruit	0.39	0.5343	0.007
Vigor	4.16	0.0448	0.052

<sup>a</sup> Data are transformed as required to impose normality.



Table 5. Slopes and confidence intervals for regressions of the number of seeds produced that escaped predation on the total number of seeds produced.

Year	Slope	99% lower	99% upper
1989	0.965	0.934	0.996
1990	0.823	0.766	0.881

responsible for the overall low fecundity observed among Aki plants. Although all plants produce many more flowers than seeds (i.e., many flowers are regularly aborted, Owen [1991b]), few plants produce many seeds. The maximum seed crops among Aki plants in this analysis were 179 and 150, in 1989 and 1990, respectively. Mean seed crops were much lower, however, at 28.6 in 1989 and 33 in 1990 (Table 1).

It is yet to be shown that the interaction illustrated here is common to other bruchid/*Astragalus* systems. It is important to note that the results reported here were recorded in an extreme environment and the ecology of these species may differ in fundamental ways in more amiable habitats. Because Aki and *A. aureolus* occur together at lower elevations (Owen 1991b), a broader investigation could be accomplished and would add to a greater understanding of the biology of both species.

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